Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia) 5. *Palaemon (Palaemon) adspersus* Rathke, 1837

A. A. Fincham
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

This study on *Palaemon adspersus* completes the descriptive part in the series of papers on the larval development of Palaemoninae found in British waters (Fincham, 1977, 1979*a*, 1979*b*, 1983). *P. adspersus* is widely distributed in shallow water (0–6 m), often in estuarine conditions, and has been recorded from as far north as the Norwegian Sea and the Gulf of Bothnia, to the Bay of Biscay in the south (Fincham & Williamson, 1978). The species is fished commercially in Danish waters (Jensen, 1958), but scarce around the British Isles (Smaldon, 1979). It is with pleasure, therefore, that I thank Dr L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie at Leiden for helping me to collect ovigerous females of *P. adspersus* from a brackish pool in the SW. of the Netherlands, from whence they were transported to the British Museum (Natural History) for rearing. Six larval and the first post larval stages are described in this paper from the laboratory rearing of *P. adspersus*.

Materials and Methods

Ovigerous *Palaemon adspersus* were collected in the SW. of the Netherlands by hand-netting in June 1980 at the edge of an 8 m deep, brackish pool, 'Inlaag 1953', situated just inland from the outer dyke of Schouwen Island (Zeeland Province) near the town of Ouwerkerk.

Similar rearing techniques to those reported previously (Fincham, 1983) were used. Water temperature was maintained at 15°C and salinity of the recirculating water system at 10‰, equivalent to those recorded in Inlaag 1953 at the time of sampling. Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1984.337.

Palaemon (Palaemon) adspersus Rathke, 1837

Cancer squilla Linnaeus, 1758
Palaemon adspersus Rathke, 1837
Palaemon fabricii Rathke, 1843
Palaemon rectirostris Zaddach, 1844
Leander rectirostris Czerniavsky, 1884
Leander adspersus var. *fabricii* De Man, 1915
Palaemon (Palaemon) squilla Holthuis, 1950
Palaemon (Palaemon) adspersus Holthuis, 1957

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. Czerniavsky, 1884. zoea 1, Figs 30, 31 (as *Leander rectirostris*); Mortensen, 1897 zoeae I–V, post larva, Plate 1, Figs 1–3, 5–8, Plates 2, 3, Plate 4, Figs 1, 3–4, plankton (as *Leander fabricii*); Kalichevsky, 1904 (as *Leander rectirostris*); Sollaud, 1923 (as *Leander adspersus*); Makarov & Golodetsky, 1980; zoeae 1–5, post larva, Figs 1–3, laboratory reared.

In the following short descriptions of the key characters of the larval stages, setal counts have been omitted usually but they are recorded in Table 1.

Table 1 Larval development and range of morphological and meristic variation in *Palaemon adspersus*. R = rudimentary; + = present/yes; − = absent/no; W = wide; N = narrow;[1] reduced setation on exopodite.

	Zoea/Moult						
	1	2	3	4	5	6	PL1
Carapace							
No. dorsal spines	0	1	2	3	3	3	3–5
No. ventral rostral spines	0	0	0	0	0	0	1–2
Supraorbital spines +/−	−	+	+	+	+	+	−
No. antero-lateral spines	0	1	2	2	2	2	2
Rostrum tip—downturned +/−	−	+/−	−	−	−	−	−
Ventral retrorse hooks +/−	+	+	+	−	−	−	−
	One group				Two groups		
Antenna 1	1W,2N	2W,2N	3W	3W,1N	3W,1N 2N	3W,1N 2N	3W 2N
Stylocerite +/−	−	R	+	+	+	+	+
Statocyst +/−	−	−	−	R	R	R	+
No. segments flagellum internal	0	0	0	0	1	1	4
external	1	1	1	1	1	1	3
Accessory flagellum +/−	−	−	−	−	−	−	−
Antenna 2							
Endopodite—No. segments	1	1	3–4	3–4	5–6	7–8	many
Length of scaphocerite	0·68:1 to 0·72:1	0·67:1 to 0·72:1	0·73:1 to 0·80:1	0·90:1 to 0·95:1	⩽	>	>
Exopodite—No. distal segments	5	4–5	3	0	0	0	0
No. plumose setae	9+2	14+2	18+2 to 20+2	21+2 to 22+23	24–26	26–28	⩾30
External spine +/−	−	−	−	−	−	−	+
Mandible—Lacinia mobilis +/−	+	+	+	+	+	+	−
Palp	−	−	−	−	−	−	−
Maxilla 1							
No. endite setae—Coxa	6	6	6	7	7	7	c.8
Basis	5	7	7	8	8	8–9	c.16
Maxilla 2							
No. endite setae—Coxa	4	4	4	4	4	4	0
Basis 1	3	3	3	3	3	3	5
Basis 2	4	4	4	4	4	4	6
Endopodite	3	3	3	3	3	3	0
No. plumose setae—Exopodite	5	7	10–11	13–16	17–19	22–24	c.26
Maxilliped 1							
No. setae on internal margin—Coxa	1	1	1	1	1	1	c.4
Basis	6	6	6	6	8	8	c.22
Exopodite no. setae—Lateral	0	0	0	0	1	3	c.7
Maxilliped 2							
Endopodite—No. of segments	4	4	4	4	4	4	5
Exopodite +/−	+	+	+	+	+	+	+
Setae +/−	+	+	+	+	+	+	+/−
Maxilliped 3							
Endopodite—No. of segments	4	4	5	5	5	5	5
Exopodite +/−	+	+	+	+	+	+	+
Setae +/−	+	+	+	+	+	+	+/−
Pereiopods 1 & 2 +/−	R	+	+	+	+	+	+
Biramous +/−	+	+	+	+	+	+	+
Endopodite—propodus fixed finger +/−	−	−	−	+	+	+	+
Pereiopod 3 +/−	−	R	R	+	+	+	+
Biramous +/−		+	+	+	+	+	+[1]

continued

Table 1 *Continued.*

	Zoea/Moult						
	1	2	3	4	5	6	PL1
Pereiopod 4 +/−	−	R	R	R	+	+	+
Biramous +/−		+	+	+	+	+	+[1]
Pereiopod 5 +/−	−	R	R	+	+	+	+
Biramous +/−		−	−	−	−	−	−
Abdomen							
Somite 5—lateral spines +/—	−	+	+	+	+	+	+/−
Somite 6—'Continuous' with Telson +/−	+	+	−	−	−	−	−
Pleopods +/−	−	−	−	R	R	R	+
Fringing setae +/−				−	−	−	+
Appendix interna 2–5 +/−				−	−	−	+
Telson							
Posterior margin concave (−)/ convex (+)	+/−	+/−	−	−	−	+/−	+
Spine formula	7+7	7+7	[1]6+ 6[1]	[1]4+ 4[1]	[1]4+ 4[1]	[1]4+ 4[1]	2+2
Small spines +/−	+	+	+	+	+	+	−
No. prs. lateral spines	0	0	0	0	0	0	2
Uropods +/−	−	−	+	+	+	+	+
Long plumose setae—Endopodite			0	9–11	15–17	18–20	23–27
Exopodite			11–12	16–19	19–22	22–24	26–30

Description of larval stages

Key characters are printed in *italic* type and are useful for separating stages in British species.

Zoea 1 (Fig. 1) 2·6 mm (2·5–2·7 mm)

Head (Figs 1a,b): *eyes sessile.*
Carapace (Figs 1a,b): *without spines, rostrum straight,* tapering distally, ventral margin with minute retrorse teeth distally, *shorter than peduncle of antenna 1.*
Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment with three aesthetascs distally, two narrow, one wide.
Antenna 2 (Fig. 1d): peduncle with short spine on inner antero-lateral corner. Exopodite as a broad lamina divided into 5 short segments distally with 9+2 plumose setae on inner and distal margins. Endopodite of one segment (0·7 length of exopodite) with terminal plumose seta and a short spine.
Mandibles (Fig. 1e): assymetrical.
Maxillipeds 1–3 (Figs 1h–j): with natatory exopodites.
Pereiopods 1,2 (Figs 1k,l): *rudimentary, biramous.*
Pereiopods 3–5: absent.
Abdomen (Figs 1a,b): *somite 5 with posterior margin rounded,* not produced into spines, somite six continuous with telson. No trace of pleopods.
Telson (Fig. 1p): fans out distally, posterior margin almost straight, bearing 7+7 spines, with minute spines between four innermost spines.

Zoea 2 (Fig. 2) 2·8 mm (2·7–2·9 mm)

Head (Figs 2a,b): *eyes stalked.*
Carapace (Figs 2a,b): *one dorso-medial and a pair of supra-orbital spines* all bent forward with small retrorse teeth, *rostrum straight with retrorse teeth ventrally at tip.*
Antenna 1 (Fig. 2c): *two peduncle segments, stylocerite forming on proximal external margin of first segment; single flagellar segment with four terminal aesthetascs, two wide and two narrow.*
Antenna 2 (Fig. 2d): exopodite with 5 short segments distally.
Pereiopods 1,2 (Figs 2k,l): *developed with natatory expodite.*
Pereiopods 3,4 (Figs 2m,n): *rudimentary, biramous.*
Pereiopod 5 (Fig. 2o): *rudimentary, uniramous.*
Abdomen (Figs 2a,b): *somite 5 with posterior margin produced into a pair of conspicuous lateral spines; somite 6 continuous with telson.*
Telson (Fig. 2p): *developing uropods visible beneath exoskeleton* alongside telson proper; *in central group of small spines, one pair longer than others.*

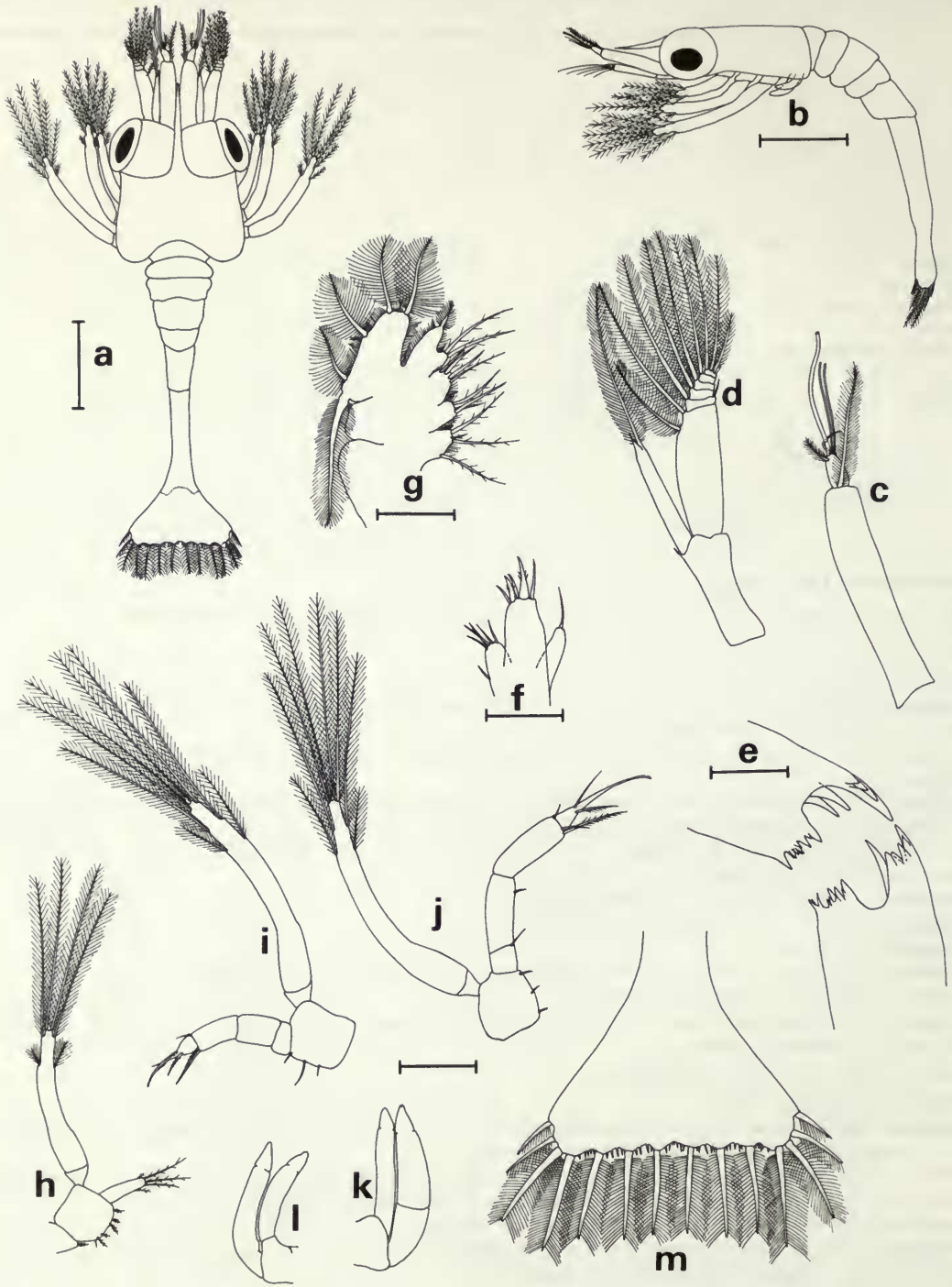

Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) telson. Bar scales: a,b = 0·5 mm; c,d, h–m = 0·2 mm; f,g = 0·1 mm; e = 0·05 mm.

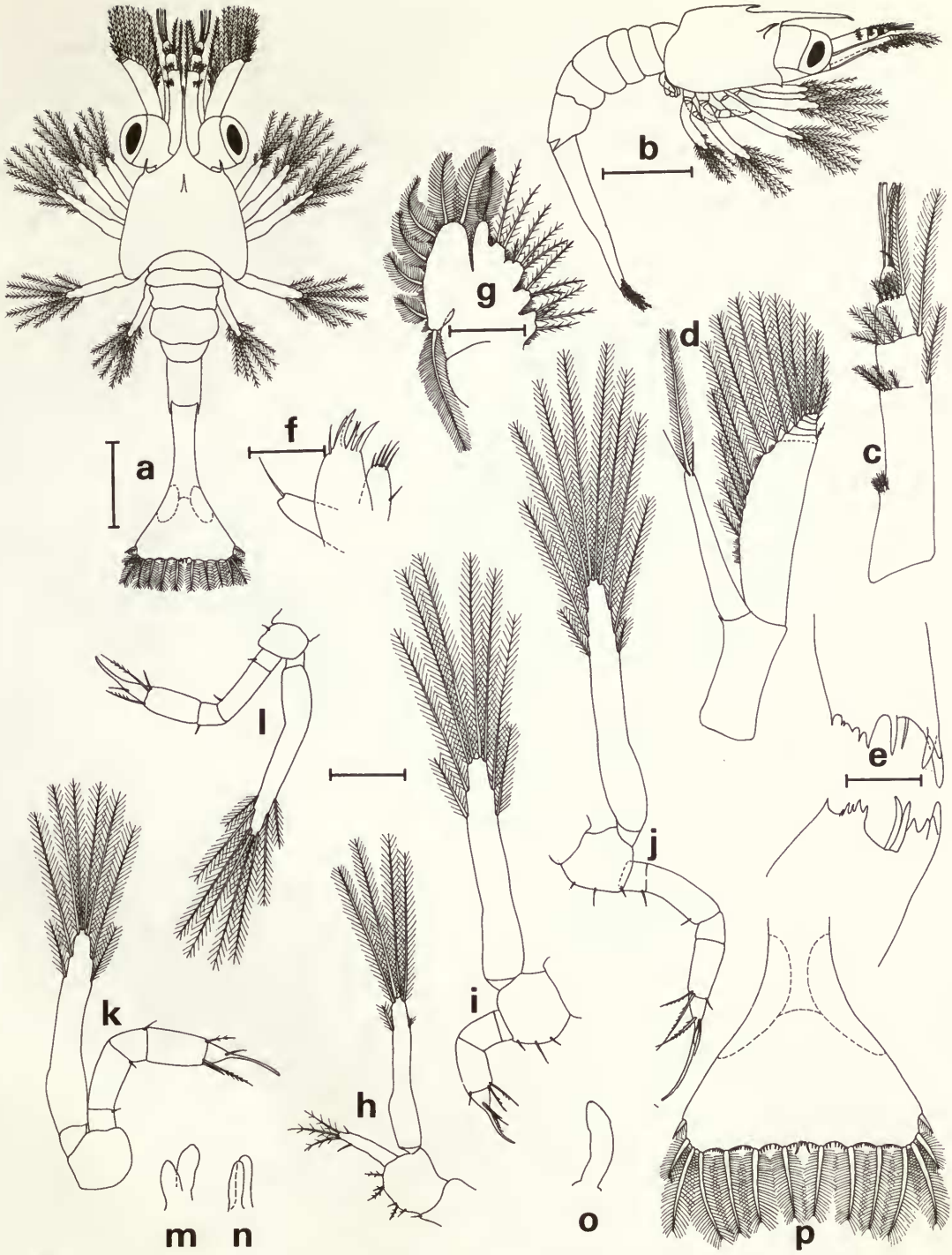

Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a,b = 0·5 mm; c,d,h–p = 0·2 mm; f,g = 0·1 mm; e = 0·05 mm.

ZOEA 3 (Figs 3,4) 3·3 mm (3·0–3·8 mm)

Carapace (Figs 3a,b): *two dorso-medial spines* and pair of small fronto-lateral spines at edge of carapace beneath eyes, former with retrorse teeth ventrally; rostrum straight with retrorse teeth ventrally at tip.
Antenna 1 (Fig. 4a): *conspicuous spine medially,* stylocerite more pronounced; distal segment of peduncle bearing *first segment of internal flagellum,* single segment of *external flagellum bearing 3 wide aesthetascs distally.*
Antenna 2 (Fig. 4b): exopodite with distal part divided into 3 short segments, *endopodite of 3 segments.*
Abdomen (Figs 3a,b, 4k): *somite 6 divided from telson by suture. Uropod endopodite rudimentary with no marginal setae, exopodite with marginal setae.*
Telson (Fig. 4k): narrower but still broader distally, outer pair of spines on posterior margin much reduced or absent on one or both sides.

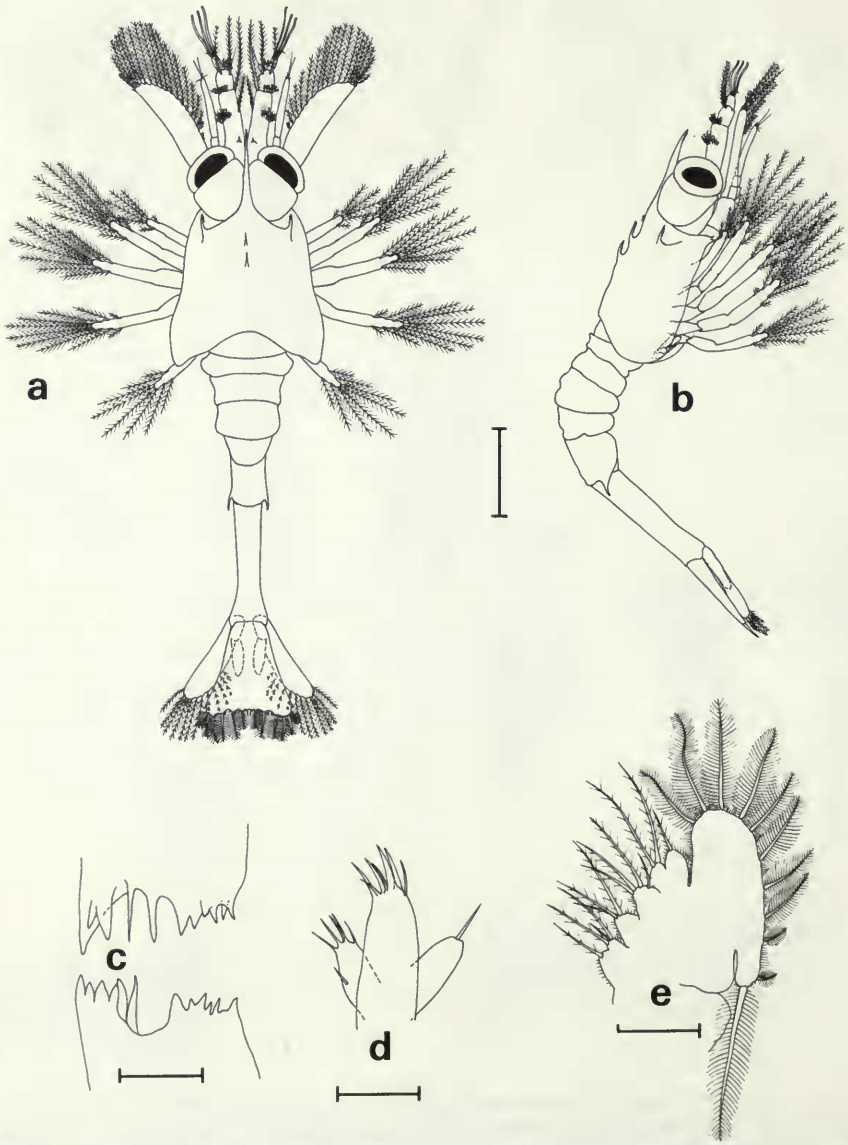

Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a,b = 0·5 mm; c = 0·05 mm; d,e = 0·1 mm.

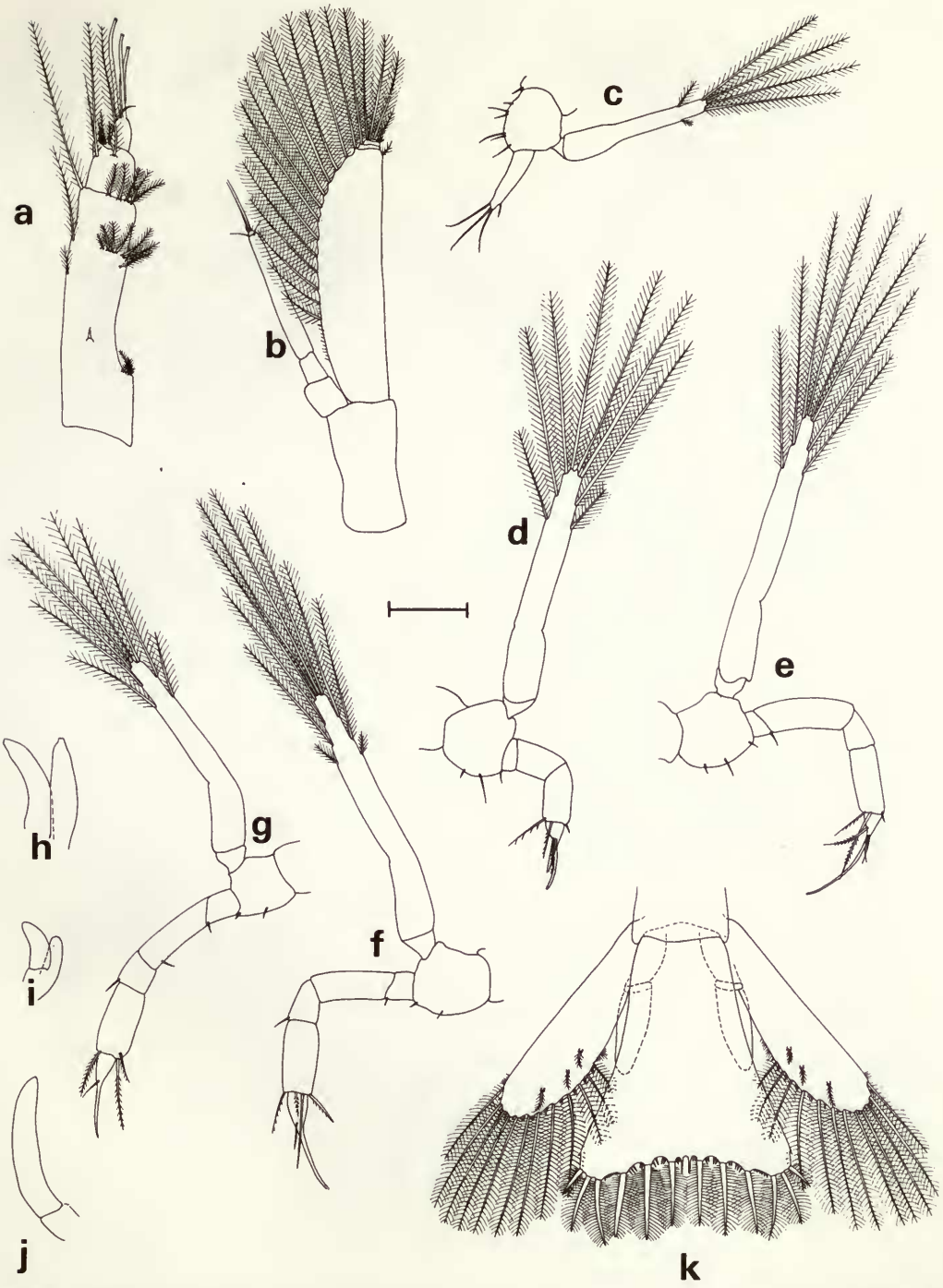

Fig. 4 Zoea 3: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale: 0·2 mm.

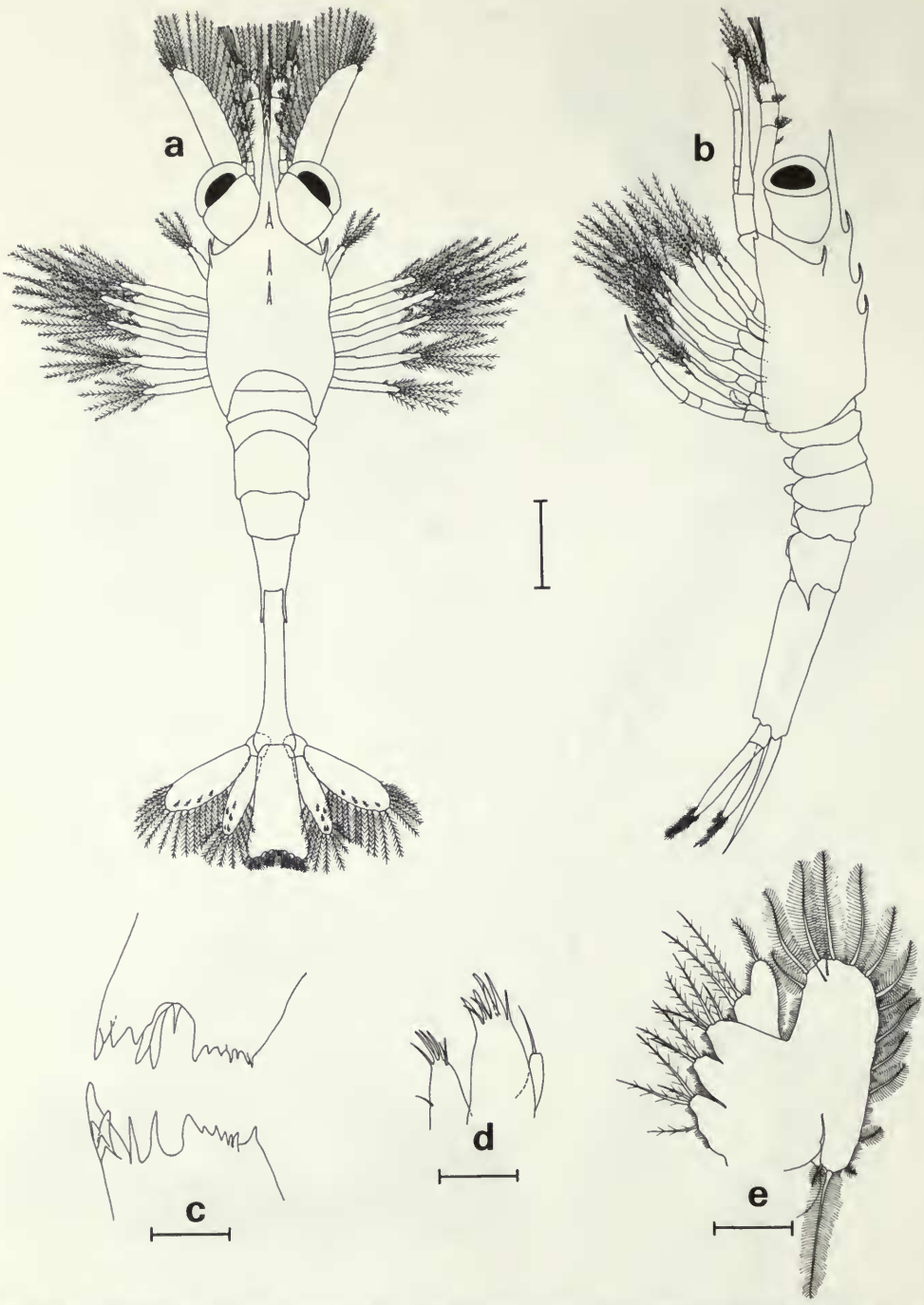

Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a,b = 0·5 mm; c = 0·05 mm; d,e = 0·1 mm.

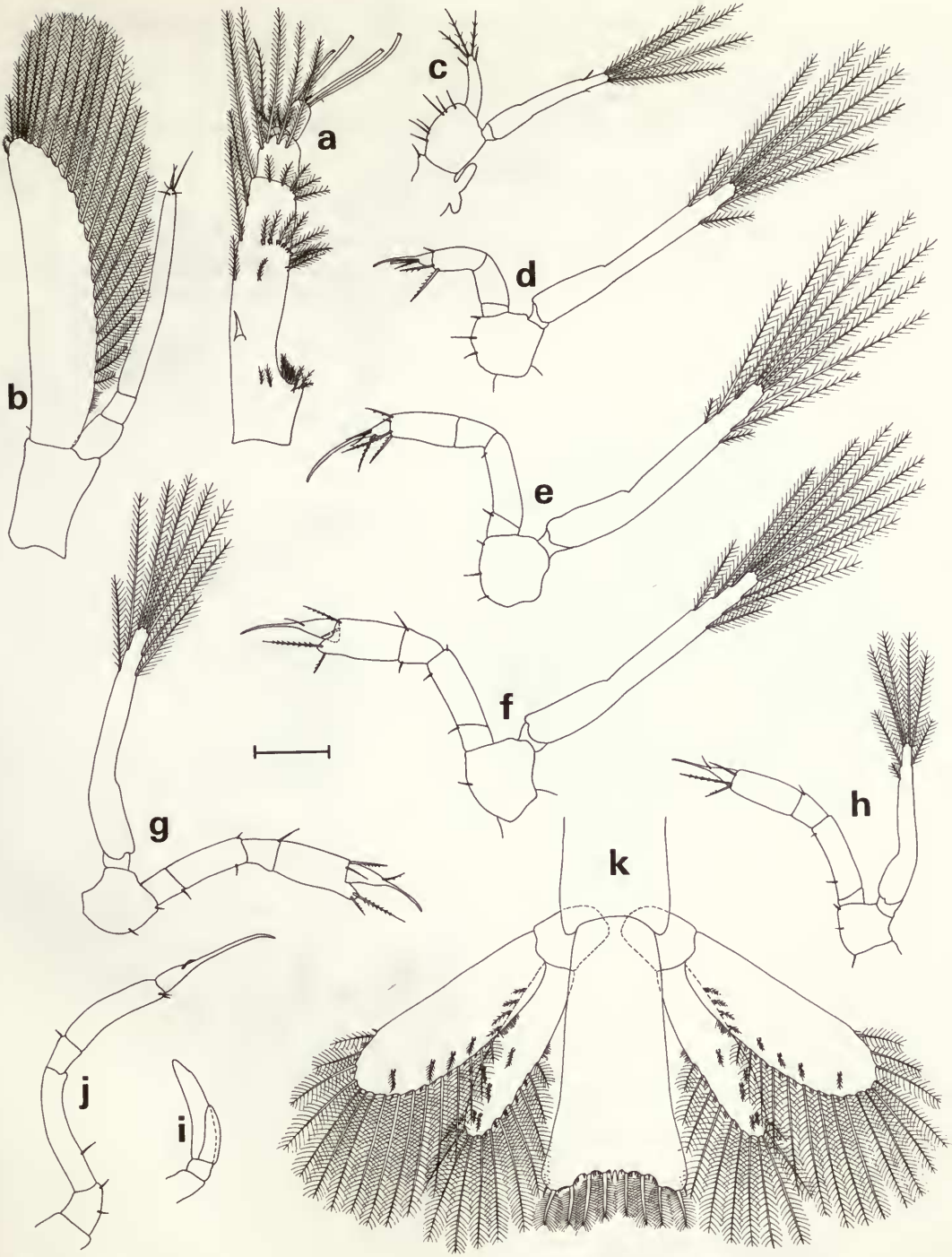

Fig. 6 Zoea 4: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale: 0·2 mm.

ZOEA 4 (Figs 5,6) 4·2 mm (4·0–4·3 mm)

Carapace (Fig. 5a,b): *three dorso-medial spines* with retrorse teeth ventrally; pair of small fronto-lateral teeth at edge of carapace beneath the eyes; *rostrum straight,* but with no retrorse teeth at tip.
Antenna 1 (Fig. 6a): *single segment of external flagellum bearing 3 wide and 1 narrow aesthetascs distally.*
Antenna 2 (Fig. 6b): distal part no longer divided into segments.
Pereiopods 1,2 (Figs 6f,g): *endopodite with internal distal margin of propodus produced slightly forward* (will become fixed finger of chela).
Pereiopod 3 (Fig. 6h): *developed with natatory exopodite.*
Pereiopod 4 (Fig. 6i): *rudimentary, biramous.*
Pereiopod 5 (Fig. 6j): *developed, uniramous.*
Abdomen (Figs 5a,b, 6k): *endopodite and exopodite of uropod both with marginal plumose setae.*
Telson (Fig. 6k): narrower, but still broader distally; posterior margin weakly concave with *4+4 large spines;* latero-distal margin spines reduced to one small pair, or a single spine on one side, or absent.

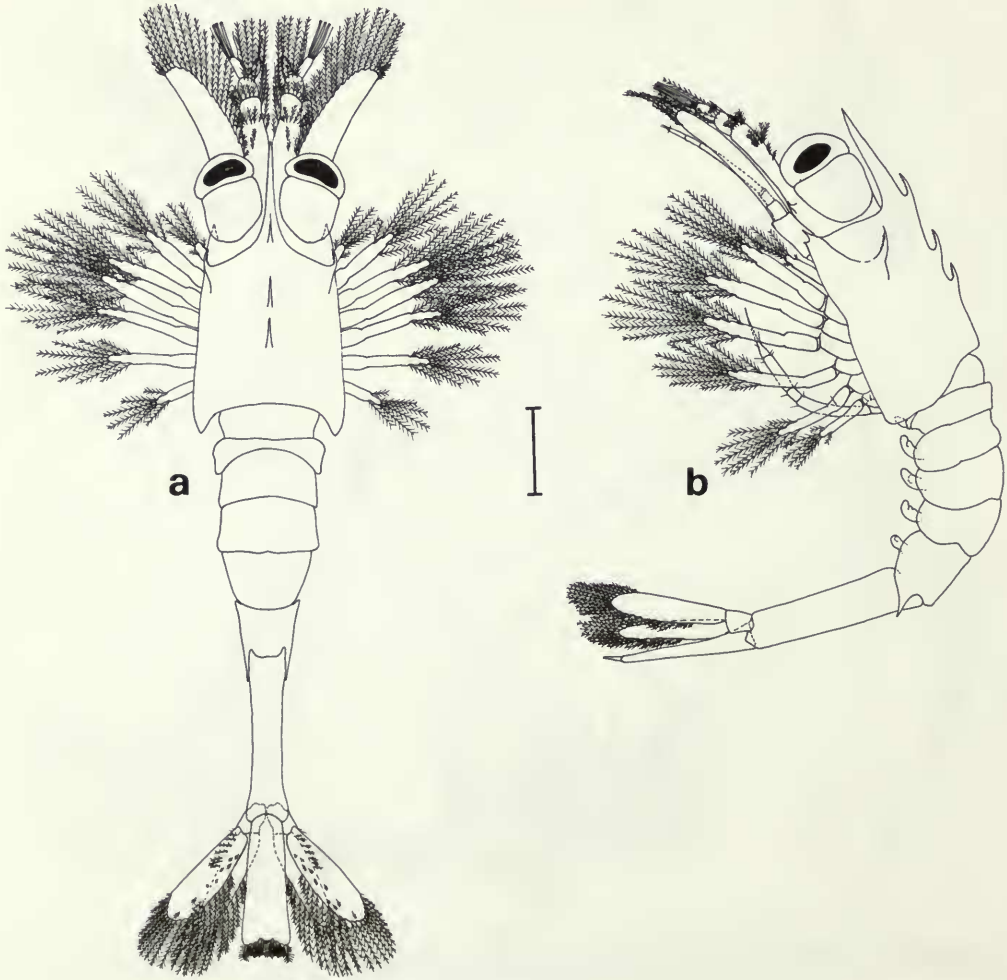

Fig. 7 Zoea 5: (a) dorsal view; (b) lateral view. Bar scale: 0·5 mm.

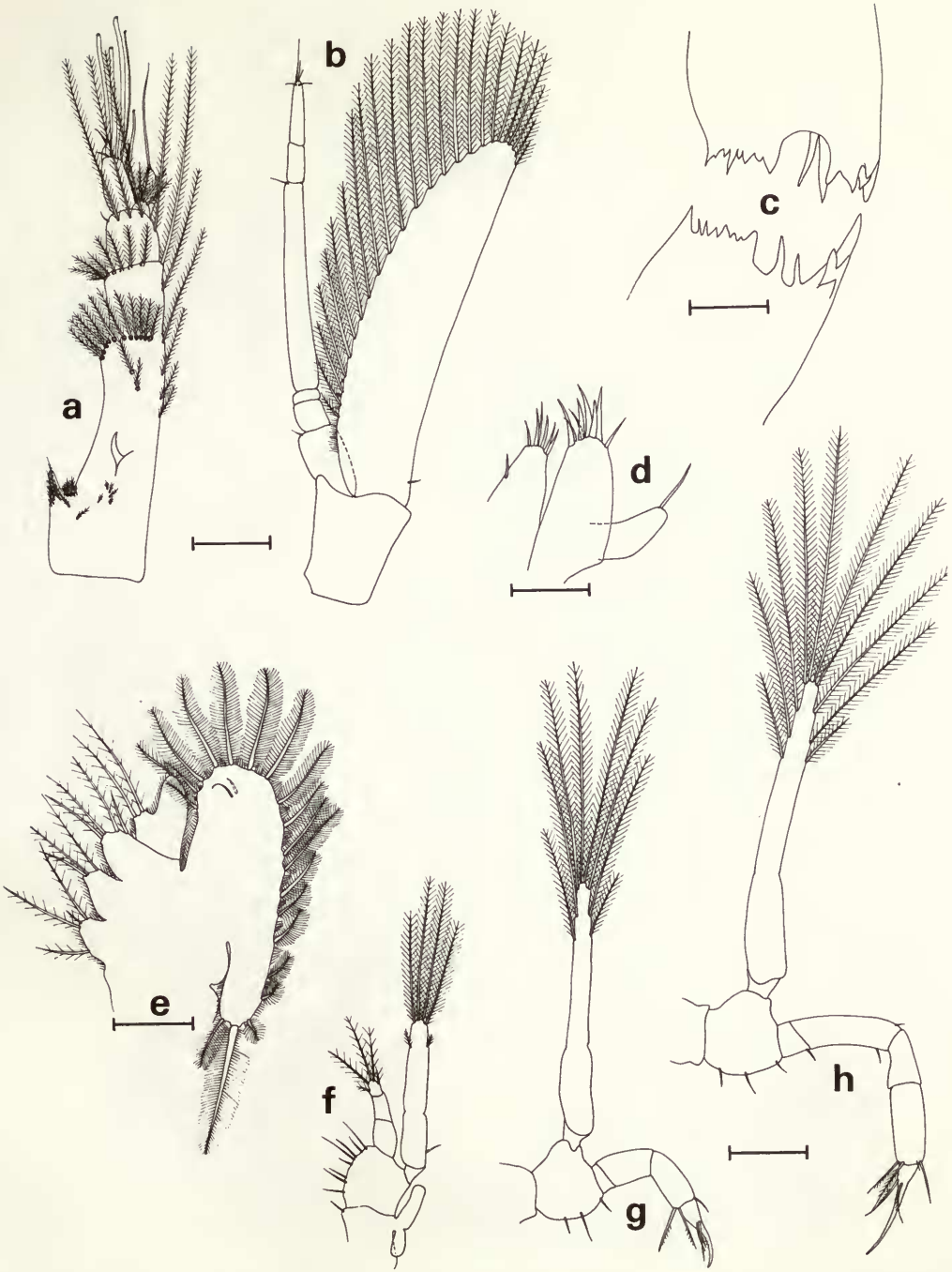

Fig. 8 Zoea 5: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a,b,f–h = 0·2 mm; c = 0·05 mm; d,e = 0·1 mm.

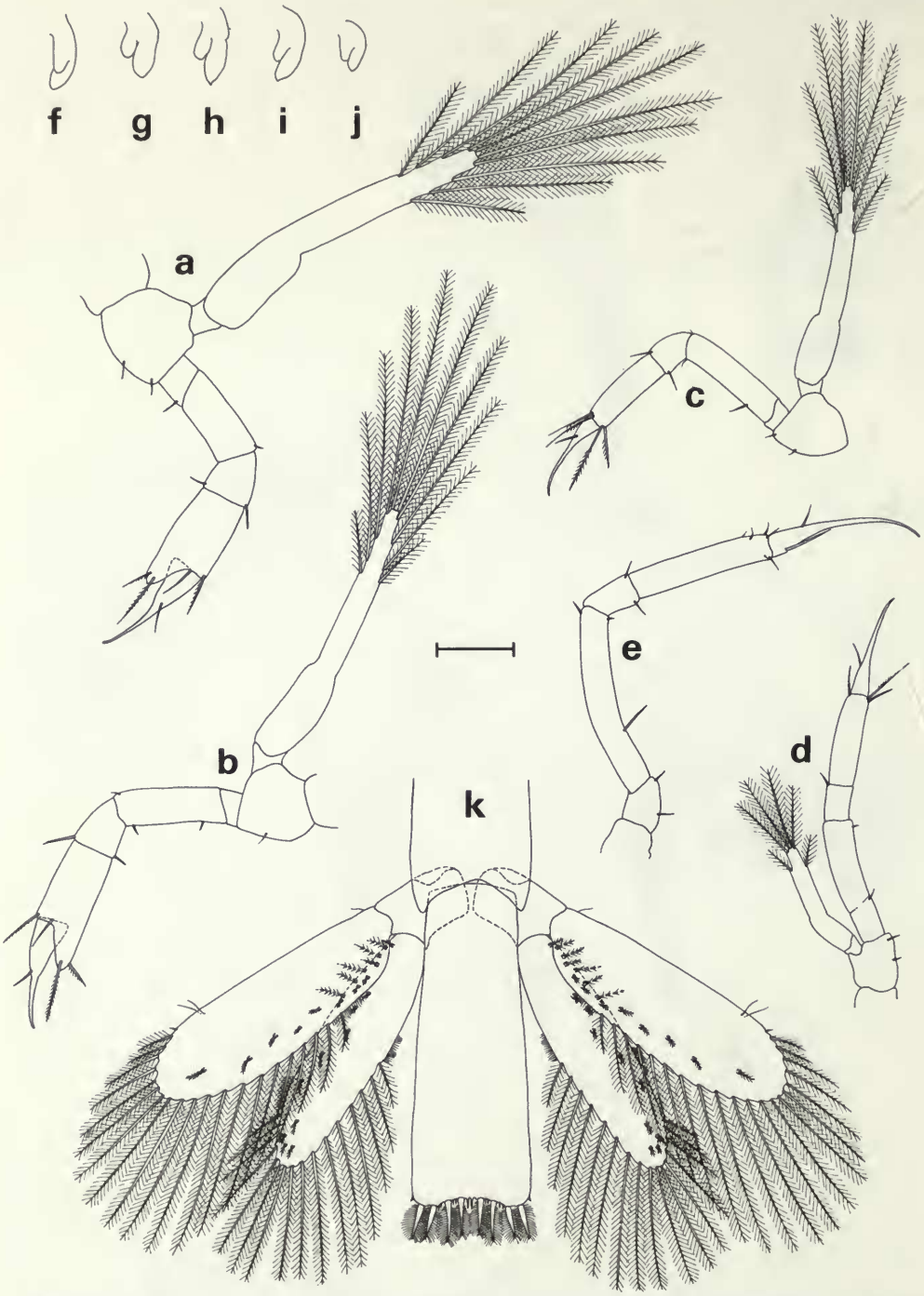

Fig. 9 Zoea 5: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) pleopod 1; (g) pleopod 2; (h) pleopod 3; (i) pleopod 4; (j) pleopod 5; (k) telson. Bar scale: 0·2 mm.

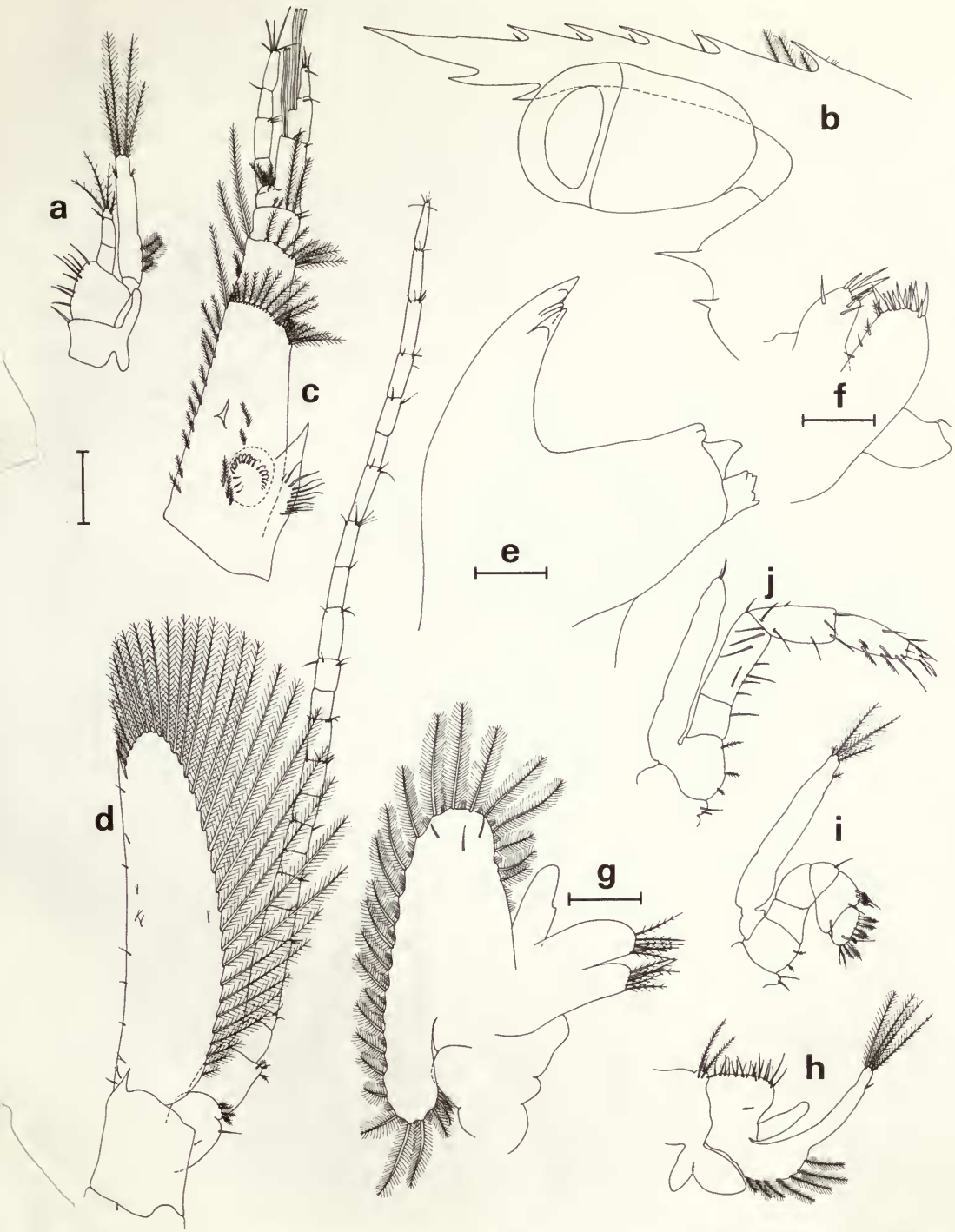

Fig. 10 Zoea 6: (a) maxilliped 1; Post larva 1: (b) rostrum and anterior of carapace; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3. Bar scales: a–d, h–j = 0·2 mm; e = 0·05 mm; f,g = 0·1 mm.

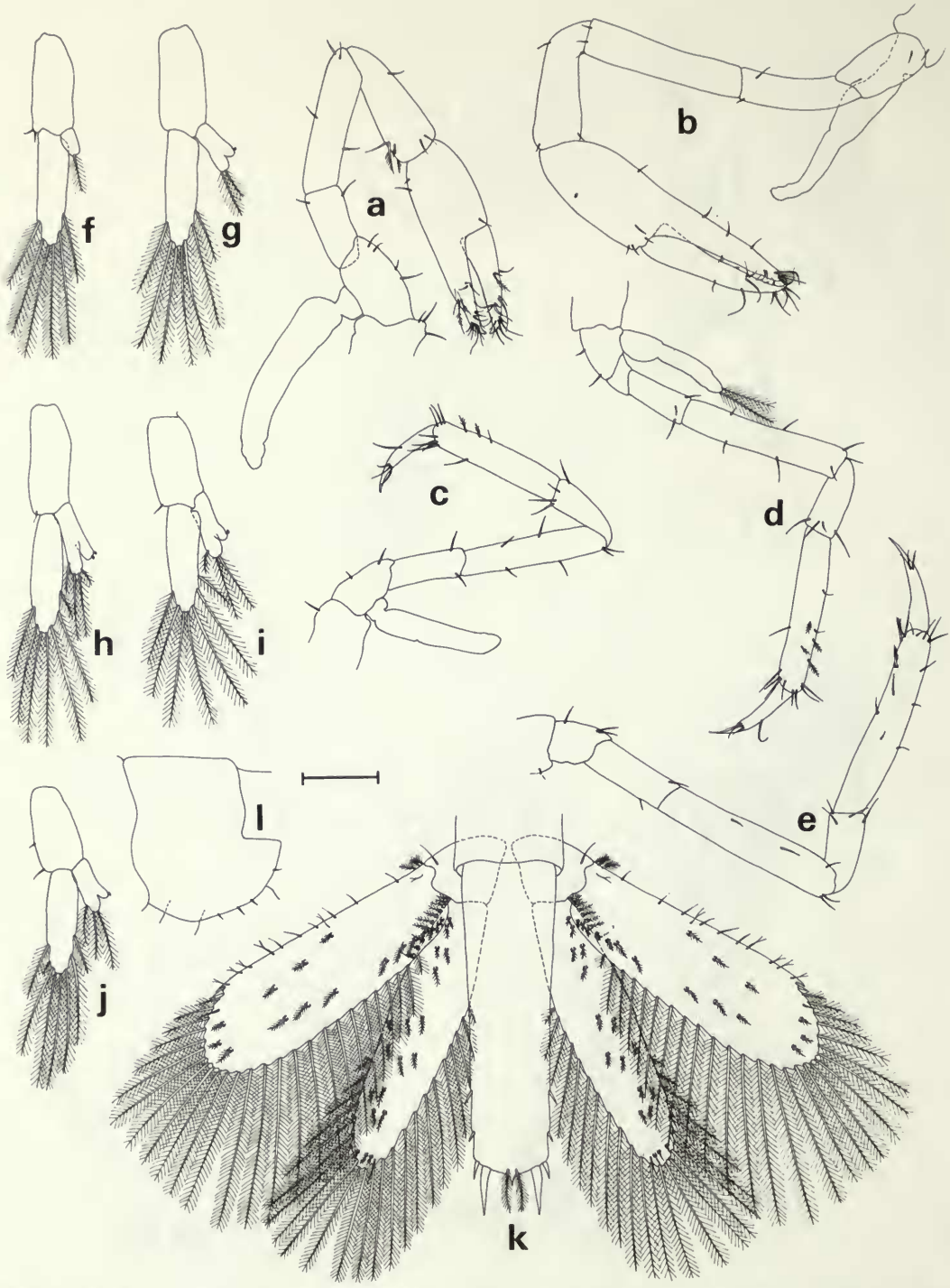

Fig. 11 Post larva 1: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) pleopod 1; (g) pleopod 2; (h) pleopod 3; (i) pleopod 4; (j) pleopod 5; (k) telson; (l) abdominal somite 5 with weak postero-lateral spine. Bar scale: 0·2 mm.

ZOEA 5 (Figs 7–9) 4·7 mm (4·5–5·0 mm)

Antenna 1 (Fig. 8a): *single segment of external flagellum bearing three wide and one narrow aesthetascs distally, additional group of 2 narrow aesthetascs on internal margin; rudiment of circular statocyst visible on first segment of peduncle.*
Antenna 2 (Fig. 8b): endopodite flagellum of about six segments, *equal to or just longer than scaphocerite in length.*
Maxilliped 1 (Fig. 8f): *8 setae on internal margin of basis,* 0 or 1 plumose seta on proximo-lateral margin of exopodite.
Pereiopods 1,2 (Figs 9a,b): *endopodite with internal distal margin of propodus produced forward to more than half length of dactylus* (excluding narrowed terminal portion).
Pereiopod 4 (Fig. 9d): *developed, exopod with fringing setae.*
Abdomen (Figs 7b, 9f–j): *rudimentary, biramous pleopods on somites 1–5.*

ZOEA 6 (Fig. 10a) 4·7 mm (4·5–5·0 mm)

Maxilliped 1 (Fig. 10a): *3–4 plumose setae on proximo-lateral margin of exopodite.*

POST LARVA 1 (Figs 10,11) 5·0 mm (4·8–5·5 mm)

Most specimens had metamorphosed to post larvae at this moult but a few specimens moulted once more before metamorphosing.
Carapace (Fig. 10b): *rostrum with 3–5 dorsal and 1–2 ventral teeth* (rostral tip straight). *Supra-orbital spines missing.*
Antenna 1 (Fig. 10c): *internal flagellum usually of 4 segments and external flagellum usually of 3 segments.*
Antenna 2 (Fig. 10d): endopodite multisegmented at least twice as long as scaphocerite.
Mandible (Fig. 10e): *divided into pars incisiva and pars molaris*; lacinia mobilis absent and palp (three-jointed in adult) not yet developed.
Maxilla 2 (Fig. 10g): complete loss of setae on coxal endite and endopodite, increase in setae on basal endites.
Maxilliped 1 (Fig. 10h): *six or more plumose setae on proximo-lateral margin of exopodite,* usually complete loss of terminal plumose setae on endopodite.
Maxilliped 2 (Fig. 10i): *endopodite with dactylus, propodus, carpus and merus flattened.*
Maxilliped 3 (Fig. 10j): endopodite dactylus shortened, terminal setae of exopodite much reduced.
Pereiopods 1,2 (Figs 11a,b): *fingers of chelae of equal length.*
Pereiopods 3,4 (Fig. 11c,d): exopodite plumose setae reduced or absent.
Abdomen (Fig. 11l): somite 5 with weak postero-lateral spines.
Pleopod 1 (Fig. 11f): *ratio of endopodite to exopodite 1:4:* endopodite uniramous, bearing single plumose seta distally, exopodite fringed with long plumose setae.
Pleopods 2–5 (Figs 11g–j): endopodite at least one-third length of exopodite, both with long plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hook(s).
Telson (Fig. 11k): *narrower distally than proximally, posterior margin tapering to a point* flanked by pair of plumose setae and two pairs of spines: two further pairs of spines on lateral margins.

Discussion

Of the five species of palaemonid known to occur in the NE. Atlantic, this is the third that occupies a brackish or estuarine habitat, the others being *Palaemonetes varians* (see Fincham 1979*a*) and *Palaemon longirostris* (see Fincham, 1979*b*). Two other NE. Atlantic palaemonids—*Palaemon elegans* and *P. serratus* (see Fincham 1977 and 1983 respectively) live in more saline littoral conditions. This probing of the freshwater habitat by some palaemonids is associated with a reduction in the number of larval stages in their life histories. *Palaemon elegans* and *P. serratus* reared in the laboratory have nine larval stages whereas *P. longirostris* and *Palaemonetes varians* have seven and five respectively, whilst six are reported here for *P. adspersus.*

Holthius (1969) reported that *P. adspersus* was first recorded from the Netherlands in 1960 from the same pool in which the present ovigerous specimens were collected. The pool was created as a result of the severe storms in 1953. A wide breach in the dyke occurred at Ouwerkerk causing extensive flooding on the island of Schouwen. Tidal currents scoured a deep creek and

after the dyke was closed in 1954 a brackish pool remained behind the dyke, with salinity stabilizing at about 11‰. It is the only known locality for *P. adspersus* in the Netherlands (Holthuis, 1969; Heerebout, 1974).

This isolated population of *P. adspersus* formed part of a recent study to quantify genetic differentiation and gene flow using electrophoretic data (Berglund & Lagercrantz, 1983). They found that the *P. adspersus* population from 'Inlaag 1953' was genetically distant from other populations tested and more monomorphic with only one variant allele in the 25 loci tested. Berglund & Lagercrantz suggested that this could be explained by 'founder' effects on small populations.

The classic ontogenetic study on *P. adspersus* by Mortensen (1897) was based on specimens from various sites in Denmark. Specimens collected by Berglund & Lagercrantz (1983) from the Danish, non-tidal Limfjord area showed less genetic variability from other Scandinavian and French sites than from the isolated Dutch population. It was particularly instructive, therefore, to compare the larval drawings made by Mortensen with those prepared for this paper.

The correlation is close, but certain differences are apparent. A comparison of sizes at each stage show Mortensen's larvae to be consistently larger: stage 1: 3·0 mm (2·6 mm, present study), stage 2: 3·0 mm (2·6 mm), stage 3: 4·5–5·0 mm (3·3 mm), stage 4: 6·0 mm (4·2 mm), stage 5: 7·0 mm (4·2 mm) and first post larva: 8·0 mm (5·0 mm). Mortensen's stage 6 is already a post larva complete with fully setose pleopods (Fig. III, 7 VI) whereas stage 6 reported here was the last larval stage with non-setose pleopods (Figs 9f–j) and setose thoracic exopods. This insertion of extra moults in palaemonid species reared in the laboratory has been noted previously (Fincham, 1977, 1979*b*, 1983). The exopodite of maxilliped 1 in PL1 in the present study is naked (Fig. 10h); Mortensen records a well-developed plumose hair (Fig. 11, 6 VI). There is still a weak spine on abdominal somite 5 in PL1 in the present study whereas Mortensen draws an entirely rounded postero-lateral margin (Fig. III, 9 VI). Mortensen's figures do not record small outer spines on the telson after stage 2; although variable, they are present on one or both sides in the present material. Some of these phenetic differences were likely to be the result of the isolation of this Dutch population of *Palaemon adspersus*.

The principal aim of the rearing programme was to produce keys for identifying, to species and stage, prawn and shrimp larvae from the plankton. An earlier attempt to produce such a key for NE. Atlantic palaemonids (Fincham & Williamson, 1978) was based in part on published descriptions that frequently proved inadequate. Early palaemonid larvae of the five species are similar and in order to separate them resort was made to a tabular matrix. Even with this cumbersome arrangement not all stages of the various species could be separated. The morphological stages in the life cycles of the five species are now sufficiently documented from specimens reared from positively identified ovigerous females to enable a subfamilial diagnosis of NE. Atlantic larval Palaemoninae to be prepared. This, together with an up-dated key will form the basis of the concluding paper in this series on palaemonid larvae.

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